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STREBLOMASTIX STRIX, MORPHOLOGY
AND MITOSIS

BY

GEORGE W. KIDDER

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Vol. 33, No. 1

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CAT. NO. 23233

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY, CALIFORNIA

1929

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ZOOLOGY.—O. A. Kofoid, J. Grinnell, and S. J. Holmes, Editors.

This series contains the contributions from the Department of Zoology, from the Scripps Institution of Oceanography (until 1927), at La Jolla, California, and from the California Museum of Vertebrate Zoology in Berkeley. Beginning in February, 1927, contributions from the Scripps Institution are issued as "Bulletins of the Scripps Institution of Oceanography, Technical Series."

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BY

GEORGE W. KIDDER

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY
Vol. 33, No. 6, pp. 109-124, plates 9, 10, 3 figures in text
Issued October 16, 1929

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY, CALIFORNIA

CAMBRIDGE UNIVERSITY PRESS
LONDON, ENGLAND

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INTRODUCTION

This paper contains a description of the morphological characteristics of *Streblomastix strix* (Kofoid and Swezy, 1919), a linear polymastigote parasite inhabiting the digestive tract of *Termopsis angusticollis* Hagen. *Streblomastix* has no close relatives among the intestinal flagellates of termites. The extremely elongated body form with the linear characteristics shown in all of its parts, even to the resting nucleus, is very unusual. Imms (1919) mentions what may be a similar form in *Archotermopsis* from India, although this organism, which he calls Species alpha, is described as being rigid, which is not true of *Streblomastix strix*.

I wish to express my appreciation for the very helpful advice and criticism given to me by Dr. C. A. Kofoid and by Dr. Harold Kirby, Jr.

MATERIAL AND TECHNIQUE

Termopsis angusticollis occurs abundantly in the San Francisco Bay region of California, and may be found in great numbers in decayed logs. The material for this study was taken from termites representing nine different colonies from Contra Costa, Alameda, and Marin counties, California. Nymphs, alates, and soldiers all had a protozoan infection of 100 per cent.

After being brought into the laboratory the termites were treated in a variety of ways. Smears were made from the normal individuals for comparison with the forms found after various treatments.

In order to free the gut of wood particles the termites were placed on a diet of filter paper. At the end of a week or ten days, smears were made by teasing out the gut in a drop of weak salt solution on a slide, fixing in hot or cold Schaudinn's, Zenker's, Flemming's, osmic vapor, or Champy's fluid and staining in Heidenhain's or Delafield's haematoxylin. Of these methods hot Schaudinn's followed by Heidenhain's haematoxylin was found to give the most satisfactory results for nuclear and cytoplasmic structures, while osmic vapor followed by Heidenhain's haematoxylin was most useful for demonstrating flagella. The Feulgen reaction, used for demonstrating the distribution of nuclear material, was found to stain cellulose with about the same intensity as chromatin. In addition to the above-mentioned fixing and staining methods, osmic vapor followed by borax carmine, osmic vapor followed by Regaud's modified haematoxylin, and osmic vapor followed by acid fuchsin and methyl-green were used with success. Neutral red and Janus green B were also used. Living material was studied both with transmitted light and dark-field illumination. Sections of the entire gut were also made in order to determine the location and means of attachment of the parasite. The gut was fixed in Bouin's fluid, sectioned, and stained in Heidenhain's haematoxylin.

Very few division stages were obtained from material taken from normal termites, so, in order to eliminate the larger Protozoa that occur in the gut of *Termopsis angusticollis* and to hasten division of the remaining individuals, the starvation process was instituted as suggested by Cleveland (1925*b*). The best results were obtained from termites starved for six to ten days, *Trichonympha* and *Leidyopsis* having disappeared by this time. By the end of the fourth day of

starvation a notable increase in the long, whip-like forms of *Streblomastix* began to take place until, by the tenth day, these forms about equaled in number the normal ones. These whip-like forms will be discussed later.

Following the suggestion of Andrew and Light (1929) numbers of termites were defaunated by the oxygen method used by Light and Sanford (1928), and then refaunated from normal individuals by canula, with varying results. Groups of termites were defaunated and were then placed with equal numbers of normal termites. One antenna of each normal termite was clipped in order to distinguish it. Natural refaunation took place as the termites are habitual fecal feeders. Through daily examinations it was found that refaunation took place from seven to fifteen days after defaunation, and that, as the Protozoa were few at the time of refaunation, many division stages were to be found.

Natural refaunation after molting took place in three to six days, a much shorter time than when the defaunation was brought about by artificial means. Many division stages were found in these natural refaunates after molting.

OCCURRENCE AND BEHAVIOR

Streblomastix is found attached to the wall of the anterior portion of the hind gut of its host by means of a holdfast organ at its anterior end, or may be found swimming freely in the lumen of the canal, as shown by cross-sections of the gut of the termite. These flagellates occur in nearly 100 per cent of all normal *Termopsis angusticollis*, except just after ecdysis, and are probably not symbionts but are true parasites, living at the expense of the other Protozoa or of the termite hosts as suggested by Cleveland (1925*b*). When free they swim by means of the anterior flagella. The normal trophozoite (fig. B, 1; pl. 9, fig. 1) corkscrews through the liquid medium in a counterclockwise direction if viewed from the posterior end. The organism is able to reverse its direction of motion and in so doing the direction of the corkscrew-turning is reversed. The flagella are waved about during swimming and are, for the most part, directed ahead of the organism, pulling the animal along and at the same time causing it to rotate. There is no contraction or change of length of the individual, but there is much turning and doubling, especially on the part of the longer individuals (fig. A, 6-8; pl. 9, fig. 3).



Fig. A. Schematic representation of the forms assumed by *Streblomastix strix*. 1-4, spindle-shaped trophozoites. 5-6, relaxed trophozoites prior to division process. 7, whip-like form, probably degenerate. 8, giant individual. $\times 1260$.

MORPHOLOGY

Streblomastix presents a very wide range of shapes and sizes. As has been previously noted (Kofoid and Swezy, 1919), it is a linear organism, the elongation of its body form being carried through to all of its structures, even to the resting nucleus.

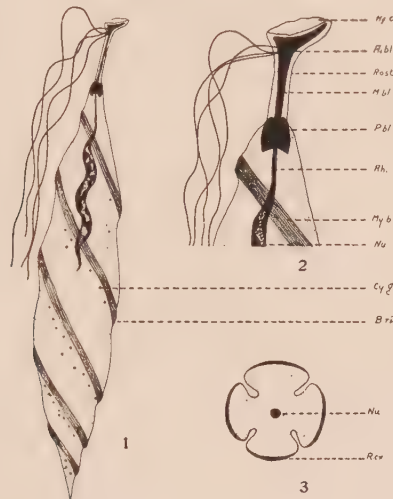


Fig. B. Diagrammatic figures of *Streblomastix strix* showing parts. 1, normal trophozoite. $\times 1500$. 2, anterior end of figure 1, enlarged. 3, cross-section of organism showing deep furrows between ridges.

Abbreviations: *a.bl.*, anterior portion of the blepharoplast; *b.ri.*, body ridges; *cy.g.*, cytoplasmic granules; *hfo.*, holdfast organ; *m.bl.*, middle portion of the blepharoplast; *my.b.*, myoneme bands; *nu.*, nucleus; *p.bl.*, posterior portion of the blepharoplast; *r.cr.*, ridge crests; *rh.*, rhizoplast; *rost.*, rostellum.

SIZE AND SHAPE

From a measurement of 300 individuals of the various forms the following size variations were obtained.

VARIATIONS IN LENGTH OF <i>Streblomastix</i>			
Type	No. measured	Range in μ	Average
All individuals	300	15 to 320	
Spindle shaped (fig. A, 1-4)	200	15 to 52	43
Whip-like (fig. A, 7)	85	45 to 320	172
Giants (fig. A, 8)	15	170 to 200	183

In breadth the range was from 2 to 15μ at the place of greatest diameter.

The rostellum (fig. B, 2, *rost.*), which may be absent in some individuals, especially those that have recently divided, ranges in length up to 15μ .

The body of the normal trophozoite is marked by distinct spirally twisted ridges, of which four to eight have been observed. The furrows between the ridges are deep and usually wider at the bottom than at the top (fig. B, 3; pl. 9, fig. 7). The direction of the twist of these ridges is from left over to right from the anterior to the posterior end. One exception to this direction of torsion was seen, a normal, closely twisted individual, 44 microns long, having a reverse, or dextrotropic torsion.

The deeply staining crests of the body ridges are made up of fine fibrils that fray off in disintegrating organisms, beginning at the posterior end (pl. 9, fig. 9). These fibrils, which are probably myonemes, run lengthwise through the outer endoplasm and are clumped in distinct bands at the crests of the body ridges. They originate in the region of the posterior part of the blepharoplast and fade out posteriorly.

The whip-like individuals have the typical form described above except that the anterior portion is elongated to many times its usual length. The myonemes have faded somewhat and the whole nuclear and flagellar apparatus is pulled far forward. These individuals I believe to be degenerate as they occur in great numbers after starvation and I have never seen any indication of division in progress.

The giant individuals occur, as do the whip-like ones, more frequently after starvation of the host and I believe they, too, represent degenerating forms. I have not seen any indication of the multiple fission described earlier (Kofoid and Swezy, 1919) in this form. The nucleus always appears as a twisted thread and I have not found it to extend posterior to the anterior sixth of the very elongated body.

CYTOPLASM

The cytoplasm is clear, showing none of the inclusions of wood so common to the other Protozoa of *Termopsis*. There is no cytostome and the organism apparently absorbs its nourishment directly from the liquid medium in which it lives.

In many individuals certain small granules appear in the posterior cytoplasm (fig. B, *cy.g.*). These tend to line up in irregular strings following the body furrows. With dark-field illumination these appear as irregular, refractile bodies and stain deeply with Heidenhain's haematoxylin after Schaudinn's fixative.

ROSTELLUM AND HOLDFAST

The cytoplasm at the anterior end is drawn out into a thin sheath or rostellum (fig. B, 2, *rost.*). This is comparable to the rostellum of the Oxymonadidae, as described by Kirby (1928). The anterior tip of the rostellum widens into a sucker-like cup, the holdfast organ (fig. B, 2, *hf.o.*), and in some individuals may be as wide as the diameter of the body. By this holdfast organ the flagellate fastens itself to the gut wall (pl. 9, fig. 5). In many individuals this holdfast is either small or entirely missing. These are the recently divided ones that are not yet equipped for an attached life. The rostellum with its holdfast is relatively rigid and in many preparations, especially after hot Schaudinn's fixative, the sheath either dissolves or remains unstained, so that the parts seen are only the anterior and middle portions of the blepharoplast. This then appears as a thread-like line with an anterior thickening from which the flagella arise.

NEUROMOTOR APPARATUS

In addition to the nucleus there are a rhizoplast, centrosome, blepharoplast, myonemes, and four anterior, free flagella. Cleveland (1925*b*) first noted correctly the number of flagella, which formerly had been given as six by Kofoid and Swezy (1919).

The rhizoplast (fig. B, 2, *rh.*) is a granular, often heavy thread connecting the blepharoplast with the nucleus. It is variable in length according to the position of the nucleus and may run for the greater part of the body length or may be very short. Owing to the pointed shape of the resting nucleus it is often difficult to determine where the rhizoplast connects. This connection is clearly seen, however, as the nucleus rounds up prior to division.

The centrosome is not seen in the resting nucleus and is only visible during mitosis, at which time it is seen as a relatively large spherule, first making its appearance at the posterior end of the nucleus.

The blepharoplast lies at the anterior tip of the body and may present a variety of forms. It is most commonly found to consist of a posterior heavy portion in the shape of an arrowhead with the barbs directed posteriorly, a narrow middle portion extending up into the sheath of the rostellum, and an anterior bulb from which the flagella arise. The blepharoplast may be so small as to appear absent in recently divided forms or may consist of one solid mass.

The flagella are four in number and are directed posteriorly along the body of attached individuals, but they may flow out in all directions in the case of the free-swimming individuals. They arise directly from the posterior portion of the anterior bulb of the blepharoplast. The flagella are rather heavy, are undifferentiated, and are of about equal length. Fixation in osmic vapor, Zenker's, or Flemming's shows them readily. They are easily observed and counted in life with dark-field illumination.

Running from the region of the posterior part of the blepharoplast and following the crests of the twisted body ridges are a number of fine fibrils. These stain heavily with Heidenhain's haematoxylin and tend to group in bands as stated above. These are the myonemes and are probably contractile. It is no doubt owing to their presence that the organism is able to bend back and forth so actively. In the earlier work on *Streblomastix* (Kofoed and Swezy, 1919) these myoneme bands were described as single myonemes between the body ridges instead of at the crests. The number given was four but this is not the case, as can be readily seen in disintegrating individuals and in cross-section. The number of bands is seen to vary from four to eight and it is possible that this number may be exceeded in some cases. The number of fine myonemes per band is very great.

NUCLEUS

The nucleus, after the usual methods of staining, is seen as a straight, wavy, or spiral rod of densely packed chromatin, tapering at both ends. When destained sufficiently it is seen to consist of an outer membrane to which are attached many irregular chromatin masses. The whole nucleus stains very densely and it is only when the cytoplasm is completely destained that any tendency to lighten is seen.

BINARY FISSION

Division of *Streblomastix* is accomplished, after a short period of nuclear reorganization, by a transverse division of the cytoplasm without any rounding up of the organism as a whole. As the stages showing mitotic figures are very few in normal host termites and relatively abundant in newly faunated individuals, it is apparent that the number of parasites remains quite constant between molts, and when this number is reduced by normal molting or by artificial means the multiplication to a certain point is rapid.



Fig. C. Diagram illustrating nuclear division in *Streblomastix strix*. The top of the figure represents the anterior end of the organism and the chromatin is represented by dots in order to clearly show the action of the centrosome and paradesmose. 1, normal nucleus. 2, rounded nucleus with centrosome on posterior end. 3, centrosome divided showing heavy paradesmose. 4-5, later stages showing migration of centrosome. 6, early telophase. 7, later telophase with constricted nuclear membrane. Note formation of thread from posterior daughter. 8-9, division nearly complete with the new set of flagella forming. 10, drawing apart of nuclei and completion of flagellar equipment. $\times 1500$.

The first evidence of mitosis is found in the nucleus, which becomes denser and begins to shorten. As the process of rounding up goes on, the cytoplasm becomes more clear and the myoneme bands begin to break up. Most of the individual myonemes become absorbed, the body ridges flatten out and the body loses its torsion. The cytoplasm often takes on a finely granular appearance (pl. 10, figs. 13 and 16).

The centrosome is not visible in the resting nucleus, but as the latter begins to round up, a very distinct spherule is seen at the posterior end of the mass of chromatin (fig. C, 2; pl. 10, fig. 10). As the posterior part of the nucleus is now in the position formerly held by the anterior part of the resting nucleus, it is possible, assuming the centrosome to have been buried at the anterior end, that the centrosome remained relatively motionless as the nucleus pulled forward in its rounding up, appearing eventually at the posterior end. Another possibility that may account for the posterior position of the centrosome in relation to the nucleus is that the centrosome may have migrated through the chromatin from the anterior to the posterior position. Still another possibility is that the centrosome arises *de novo* during the rounding up process.

The nucleus now takes the form of a spindle with the chromatin arranged in twelve to fourteen blobs. The centrosome divides and one daughter centrosome starts its migration toward the anterior end, stringing out a very heavy paradesmose between the two (fig. C, 3; pl. 10, fig. 13). The blobs of chromatin were never seen to form in any definite order but the chromatin mass remains in a coarsely granular or condensed condition throughout the period of centrosome activity. The centrosomes grow farther apart (fig. C, 4 and 5) until one is seen to lie at each end of the spindle-shaped nucleus with the heavy paradesmose visible on the surface of the nuclear membrane.

The chromatin grows more condensed and division of the mass takes place, approximately half of the chromatin going to each pole. The paradesmose persists (fig. C, 6) and the nuclear membrane constricts (fig. C, 7). The two daughter nuclei then assume the characteristic spindle shape and start elongating and pulling apart (fig. C, 9). At this time or a little later the centrosomes are lost from view in most of the cases. In a few instances (pl. 10, fig. 18) they may remain visible, connected by the paradesmose, after the nucleus has divided. During all this nuclear activity there is no apparent change in the organelles or cytoplasm but as the posterior daughter nucleus migrates away from the anterior end, a heavily staining thread is seen to be preceding it at a more rapid rate of growth (fig. C, 8; pl. 10, fig. 18). This thread is to be the new rhizoplast. It is seen to grow to the posterior end of the body and from its tip two, and then two more flagella grow out (fig. C, 9 and 10). This second set of flagella is completed before any signs of plasmotomy appear and in many cases before the nuclei pull apart (pl. 10, fig. 20). The time

required for plasmotomy seems to be relatively long as many individuals are seen with a duplication of organelles but no constriction of cytoplasm. The author has observed plasmotomy in progress and the organism whipping about in an attempt to separate in the constricted middle region, the separation being still incomplete after seventy minutes, when the organism disintegrated through drying.

That the new blepharoplast grows out from the divided posterior part of the nucleus and does not arise by a splitting of the original blepharoplast is evidenced by the normal appearance of the latter at all times during division, and by the clear cases of the growing out of the thread from the nucleus.

The cytoplasm constricts more and more until what may be spoken of as the posterior organism pulls away from the anterior organism, which presumably may remain attached to the gut lining. The former then completes the development of its blepharoplast and becomes equipped with a full set of myonemes, which clump together at the crests of the newly forming ridges. As the organism becomes more mature it begins to show marked torsion, and at the same time a lengthening of the anterior tip into a rostellum, from which develops the holdfast organ. It is now ready to fasten itself to the gut wall.

In the meantime the anterior organism is reorganizing by growing out new myoneme bands, forming ridges, and undergoing torsion. The nucleus has, by this time, assumed its elongated resting form.

No evidence of multiple fission was seen by the writer. No cyst formation was noted, infection presumably taking place by the ingestion of fresh fecal material on the part of the termite host, as noted above.

RELATIONSHIPS

Streblomastix belongs to the family Streblomastigidae of the order Polymastigida. Reichenow (1928) places it with *Pyrsonympha*, pointing out that the elongate, deeply staining structure may be, in reality, an axostyle, the nucleus not having been found. It is, however, evident that this structure is the nucleus.

Family STREBLOMASTIGIDAE Kofoid and Swezy, 1919

Polymastigida with spiral myonemes, small number of free anterior flagella, and habit of attachment.

Streblomastix (Kofoid and Swezy, 1919) emend.

Streblomastigidae with four undifferentiated flagella, four or more body ridges, and four or more myoneme bands. Type species *Streblomastix strix* (Kofoid and Swezy, 1919) emend.

Streblomastix strix (Kofoid and Swezy, 1919) emend.

Streblomastix with four to eight prominent body ridges between which are deep furrows, an elongate nucleus which rounds up and divides long before plasmotomy, a blepharoplast commonly seen as three parts—a posterior portion in the shape of an arrowhead, an elongate middle portion, and an anterior bulb from which the four flagella arise. The direction of torsion is leiotropic. This flagellate is found in the intestine of the termite *Termopsis angusticollis* Hagen from California.

SUMMARY

1. *Streblomastix strix*, from the termite *Termopsis angusticollis* Hagen, is a spindle-shaped flagellate with an average size of about 45×10 microns.

2. It is found attached to the gut wall of the termite by a cup-like holdfast organ at the tip of an elongated rostellum.

3. It has no cytostome and takes its nourishment by absorption.

4. Mitosis and binary fission occur rarely in normal hosts but occur readily in newly faunated hosts.

5. Division is accomplished by a rounding up and parting of the nucleus prior to plasmotomy, which takes place in a transverse plane.

6. *Streblomastix strix*, the type species of the family Streblomastigidae of the order Polymastigida, is characterized by having four free, undifferentiated, anterior flagella, four to eight ridges wound around the body leiotropically, myoneme bands, an elongate body form and nucleus, and an organ of attachment.

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EXPLANATION OF PLATES

PLATE 9

All figures are of *Streblomastix strix*, made with camera lucida except figs. 9 and 20. Abbreviations for methods of preparation: *S.* Schaudinn's fixative; *O.* osmic vapor; *B.* Bouin's fixative; *H.* Heidenhain's haematoxylin; *D.* Delafield's haematoxylin.

Fig. 1. Surface view of normal trophozoite showing body ridges, rostellum, and holdfast organ. O.D. $\times 1650$.

Fig. 2. Optical section of trophozoite. O.D. $\times 1650$.

Fig. 3. Whip-like individual. S.H. $\times 1650$.

Fig. 4. Giant individual. S.H. $\times 1650$.

Fig. 5. Parasites attached to the gut wall by means of the holdfast organ. B.D. $\times 825$.

Fig. 6. Rostellum and holdfast organ. O.H. $\times 1650$.

Fig. 7. Optical cross-section of an eight-ridged individual at the level of the nucleus. S.H. $\times 1650$.

Fig. 8. Same of smaller six-ridged organism posterior to the nucleus. S.H. $\times 1650$.

Fig. 9. Parasites fraying out in disintegration. Drawn from life. $\times$ about 825.



PLATE 10

Plate 10. Rounding nucleus showing centrosome and clear area in cytoplasm. S.H. $\times 1650$.

Fig. 11. Later stage than fig. 10. Centrosome divided and daughter buried in dense chromatin. S.H. $\times 1650$.

Fig. 12. Chromatin massed into definite blobs. Same stage as figure 11. S.H. $\times 1650$.

Fig. 13. Centrosome divided with paradesmose between. S.H. $\times 1650$.

Fig. 14. Centrosome at either end of nucleus with paradesmosé between. S.H. $\times 1650$.

Fig. 15. Telophase with paradesmose showing. S.H. $\times 1650$.

Fig. 16. Early telophase. S.H. $\times 1650$.

Fig. 17. Slightly earlier than figure 14. S.H. $\times 1650$.

Fig. 18. Divided nucleus. Centrosomes still visible and thread growing from posterior daughter nucleus. S.H. $\times 1650$.

Fig. 19. Just prior to plasmotomy. S.H. $\times 1650$.

Fig. 20. Organism with but two of the four new flagella developed. Drawn from life. $\times$ about 825.



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